JOURNAL OF AGRICULTURAL RESEARCH

VOL. 72 WASHINGTON, D. C., MAY 1, 1946 NO. 9

LATEX-TUBE AREAS OF THE ROOTS AND LEAVES OF THE RUSSIAN DANDELION[1]

By EDWARD F. WOODCOCK

Associate professor of botany, Michigan State College of Agriculture and Applied Science

INTRODUCTION

The distribution of the latex tubes and their appearance in cross section of the root of the Russian dandelion (*Taraxacum kok-saghyz* Rodin) have been shown by Artschwager and McGuire [2] in their morphological and anatomical studies of this plant. The object of the present investigation was to determine whether the percentage of latex-tube area in any one plant is sufficiently uniform in its various roots and leaves to justify the collection in the field of one leaf and one secondary root for the determination of latex-tube area. A technique was developed for this work by which the latex tubes could be clearly differentiated in the cross sections and thus could be easily counted and measured with the microscope.

TECHNIQUE USED IN THE INVESTIGATION

1. Segments of roots and petioles 3 mm. in length were fixed 24 hours in Flemmings fluid (1 percent chromic acid 50 cc., 10 percent acetic acid 10 cc., 2 percent osmic acid 10 cc., distilled water 30 cc.). Air was pumped out of the segments when they were first placed in the fixing solution.
2. Washed 12 hours in running water.
3. Placed in 50 percent alcohol until ready for sectioning.
4. Sections cut on a hand microtome, the thickness of the sections ranging from 60 to 70 microns.
5. Stained 12 hours in saturated Calco Oil Blue NA in 50 percent ethyl alcohol.
6. Washed in water.
7. Mounted in Clearcol.

Since in the root the latex tubes are quite uniformly distributed in the region surrounding the xylem core, the tubes were counted in a quarter of that region and the number multiplied by 4 to get the total number of tubes in the entire cross section. The diameter of 30 tubes selected at random was obtained by the use of an eyepiece micrometer scale and these diameters were used in getting the average tube area. By multiplying the average tube area by the number of tubes, the total latex tube area was obtained. The total area of the cross section was calculated. By using the total cross-sectional area and the total latex-tube area the percentage of latex-tube area was obtained. The size of the tubes in the different regions outside

[1] Received for publication October 24, 1944. This report is based upon investigations carried on by the author between June 20 and September 20, 1943, as Bankhead-Jones Project 1K of the Botanical Section of the Experiment Station of Michigan State College.

[2] ARTSCHWAGER, E., and MCGUIRE, R. C. CONTRIBUTION TO THE MORPHOLOGY AND ANATOMY OF THE RUSSIAN DANDELION (TARAXACUM KOK-SAGHYZ). U. S. Dept. Agr. Tech. Bul. 843, 24 pp., illus. 1943.

the xylem core varied, the smaller tubes being next to the xylem core and next to the periderm, and the larger tubes in the intermediate region (fig. 1, *A*).

For studying the latex tubes in the petiole (fig. 1, *B*), basal segments 3 mm. in length were fixed. Ten leaves were selected at random from each plant and about 50 sections were cut from the segment of the petiole of each leaf and mounted at random on a side. The number of latex tubes was determined in the midvein of 20 sections selected from the 50 sections. In making the selection for counting the latex tubes a mechanical stage was used. The sections were selected in sequence as they moved across the field.

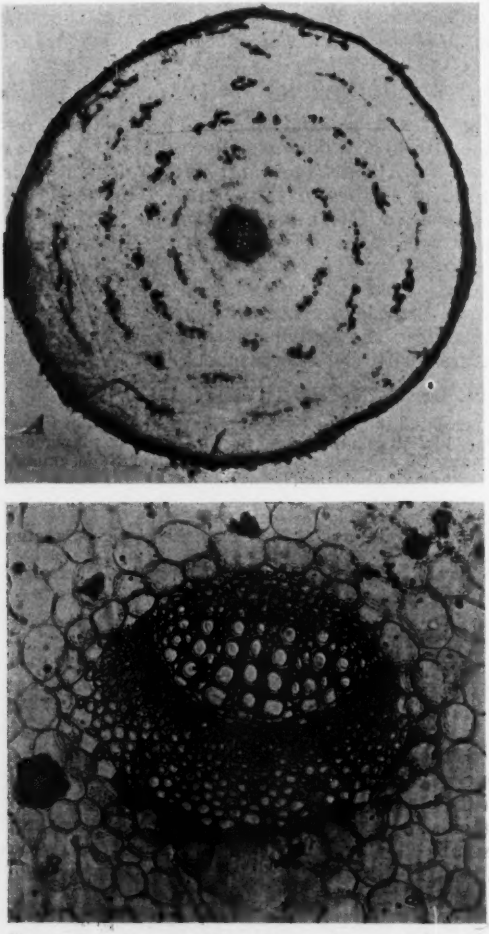

FIGURE 1.—*A*, cross section of secondary root, showing distribution of latex tubes; *B*, cross section of midvein of petiole, showing distribution of latex tube in the form of an arc along the edge of the phloem.

PRESENTATION OF RESULTS

The results of the investigations are shown in tables 1 to 3. A comparison of the number of latex tubes in 10 leaves taken from 1 plant is shown in table 1. The percentage of latex-tube area at various levels in the primary root is shown in table 2. A comparison of the total latex-tube area in the primary root with that in its large secondary roots is shown in Table 3, and this table also shows the total latex-tube area in the 7 secondary roots arising from a primary root.

The 10 leaves from a single plant showed a marked variation in the number of latex tubes in each midvein of the 10 petioles and also at various levels in the same petiole; for example, as shown in table 1, the number of latex tubes in the midvein of the petiole of 10 leaves

ranged from 2 to 29. In similar group of 10 leaves from another plant the range was 8 to 25. In a primary root there is evident a variation in the total latex-tube area at various levels, as shown in table 2, the greatest being 31 mm. from the crown. A comparison of the total latex-tube area in the primary root with that in its secondary roots showed a marked variation; for example in table 3 the primary root had 0.16 percent latex-tube area while its 5 secondary roots had from 0.27 to 2.06 percent. Similar observations of primary and secondary roots in other Russian dandelion plants showed the following: Primary 0.84 percent, its 3 secondaries 0.71 to 1.09 percent; primary 1.35 percent, its 3 secondaries 0.43 to 1.35 percent; primary 0.96 percent, its 5 secondaries 0.6 to 1.03 percent; primary 0.7 percent, its 2 secondaries 0.76 and 0.86 percent; and primary 0.68 percent, its 5 secondaries 0.16 to 1.89 percent. In table 3 the 7 secondary roots arising from 1 primary root showed a variation in latex-tube area ranging from 0.14 percent to 1.56 percent.

TABLE 1.—*Number of latex tubes in cross section of midvein of petioles of 10 leaves taken from 1 plant*

Leaf No.	Latex tubes in section No.—																				Average
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1	19	15	15	15	13	14	16	13	18	19	16	15	16	12	14	19	14	2	9	6	14
2	18	11	14	17	12	16	15	13	16	20	13	16	16	18	18	17	22	17	14	11	16
3	8	15	11	16	14	14	11	14	10	15	12	14	15	15	12	10	10	15	12	13	13
4	13	15	15	18	19	13	20	21	11	18	16	14	19	14	14	10	18	13	13	21	16
5	21	11	25	13	29	16	17	25	15	22	20	10	8	11	14	8	18	22	18	16	17
6	14	14	6	10	6	19	15	21	19	12	20	13	19	22	14	17	16	10	9	8	14
7	12	16	16	14	18	13	14	17	16	14	20	20	22	13	23	21	18	23	24	14	17
8	21	13	15	18	20	14	18	24	22	15	18	23	21	13	14	15	16	23	22	24	18
9	16	19	19	18	21	19	18	12	18	16	17	19	18	18	13	17	18	16	19	16	17
10	8	8	22	17	13	12	17	22	9	21	16	9	13	19	18	17	14	12	11	10	14
Average																					15.6

TABLE 2.—*Total latex-tube area at different levels in the same primary root*

Distance from crown (mm.)	Area of root section	Number of latex tubes	Average area of latex tube	Total area of latex tubes	Percent of latex-tube area in cross section
	a^2		a^2	a^2	
3	8, 272, 571	628	25	15, 769	0.19
6	9, 142, 798	532	33	16, 222	.18
9	8, 702, 245	544	38	20, 705	.23
12	7, 648, 457	456	31	13, 999	.18
15	6, 478, 166	564	36	20, 524	.33
18	6, 089, 522	588	44	25, 731	.42
21	6, 662, 656	556	24	13, 511	.20
25	6, 662, 656	420	28	12, 007	.18
28	6, 089, 522	476	43	20, 706	.34
31	7, 445, 858	572	69	39, 577	.53

TABLE 3.—*Total latex-tube area in the primary root and its secondary roots and in the secondary roots arising from 1 primary root*

PRIMARY ROOT AND ITS SECONDARY ROOTS

Part of root system	Area of root section	Number of latex tubes	Average area of latex tube	Total area of latex tubes	Percent of latex-tube area in cross section
	μ^2		μ^2	μ^2	
Primary root	18,430,888	1,828	107	195,925	0.16
Secondary A	1,461,032	196	91	17,914	1.23
Secondary B	13,810,857	228	166	37,734	.27
Secondary C	1,190,834	180	184	33,197	2.03
Secondary D	7,957,455	412	167	68,858	.87
Secondary E	2,531,917	376	138	52,046	2.06

SECONDARY ROOTS ARISING FROM 1 PRIMARY ROOT

Secondary A	5,190,017	504	141	81,099	1.56
Secondary B	7,270,815	484	138	66,826	.92
Secondary C	4,302,257	296	93	27,590	.64
Secondary D	2,228,719	252	125	31,467	1.41
Secondary E	3,634,303	456	125	57,091	.15
Secondary F	4,830,873	500	101	50,430	.14
Secondary G	4,302,257	364	102	36,957	.85

SUMMARY

A study of the Russian dandelion has been made to determine (1) the number of latex tubes in petioles of different leaves from the same plant, (2) the total latex-tube area at different levels in the same primary root, (3) the total latex-tube area in the primary root as compared with that in its secondary roots, and (4) that in the secondary roots arising from a single primary root.

The results of these studies fail to show any trend that would enable one to determine the total latex-tube area in a root system by examination of the primary or one secondary root of the system or one petiole of the plant.

SOME ASPECTS OF THE AERIAL DISSEMINATION OF SPORES, WITH SPECIAL REFERENCE TO CONIDIA OF SCLEROTINIA LAXA [1]

By E. E. WILSON, *associate plant pathologist*, and G. A. BAKER, *assistant statistician*
California Agricultural Experiment Station [2]

INTRODUCTION

Spread of the brown rot blossom disease by means of air-borne conidia of the casual fungus *Sclerotinia laxa* Ader. and Ruh. from well-defined centers of infection has been observed in at least 15 apricot orchards in California during the past 5 years. In 7 of these the number and disposition of the trees furnishing and receiving the conidia were such that the incidence of blossom infection could be compared quantitatively at different distances from the nearest source trees. Attempts were then made to determine the major factors influencing wind dissemination of spores, and to correlate the results with the data on disease spread.

ADAPTATION OF SCELEROTINIA LAXA TO WIND DISSEMINATION

Conidia of *Sclerotinia laxa* are produced on sporodochia which develop in large numbers during late winter on blossoms and twigs infected the previous spring. According to measurements made during these studies, the spores average 14μ long and 12μ broad. When mature they were detached from the sporodochia in fairly large numbers by an air current moving at 2.4 m. p. h. In one test conducted according to the method outlined by McCubbin (*11*)[3], their rate of settling in still air averaged about 0.36 cm. (0.14 inch) per second. Accordingly, conidia liberated at a height of 6 feet and falling freely (not affected by cross currents in the air stream) would be carried about 3,770 feet from the source by a 5 m. p. h. wind before reaching the ground. Because wind movement is seldom steady enough to permit a free fall, such a comparison is useful only to illustrate the ease with which even a gentle breeze may carry the spores. Updraughts moving at a rate slightly greater than the spores' terminal velocity will bear them upward and so permit their dissemination over great distances. There is ample evidence regarding the great distances to which spores much larger than those of *S. laxa* are carried by air currents (*12*).

[1] Received for publication October 2, 1944.
[2] Grateful acknowledgment is due Dr. F. A. Brooks, California Agricultural Experiment Station, for advice concerning atmospheric properties: to Dr. Katherine Esau, California Experiment Station, for translating Stepanov's article; and to Dr. K. Starr Chester, Oklahoma Agricultural and Mechanical College, for translating Boevsky's paper.
[3] Italic numbers in parentheses refer to Literature Cited, p. 326.

SPREAD OF THE BROWN ROT BLOSSOM DISEASE IN APRICOT ORCHARDS

During the testing of monocalcium arsenite (*20*) as an eradicant spray against the conidia of *Sclerotinia laxa*, fairly large blocks of apricot (*Prunis armeniaca L.*) trees were rendered comparatively free [4] of inoculum. Since the spray was applied in January, it gave little or no protection to blossoms; and whenever air-borne conidia were brought into the sprayed trees from nearby sources, blossom infection developed abundantly (*20*). In such cases gradients of blossom infection developed in the recipient trees (sprayed) adjacent to the source trees (unsprayed).

GRADIENTS OF BLOSSOM INFECTION IN THE VICINITY OF SPORE SOURCES

In 1939 three and in 1940 four such gradients were studied in the Sacramento Valley. Data on the amount of blossom infection were secured in each recipient and each source tree in these areas. Figure 1 illustrates the situation in one orchard. The recipient trees adjoined the source trees on the north, east, and south. In trees east, southeast, and south of the source, never more than 1 percent of the blossoms

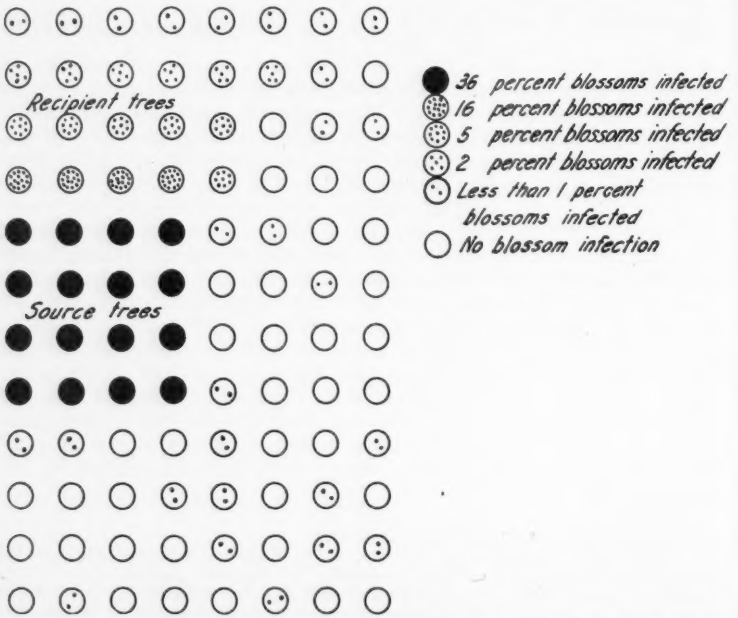

FIGURE 1.—Gradations in the amount of blossom infection by *Sclerotinia laxa* in inoculum-free (recipient) apricot trees located at different distances north of trees (source) in which conidia of the fungus were abundant.

[4] Free of inoculum in the sense that the number of effective conidia remaining in the trees sprayed with monocalcium arsenite incited only insignificant amounts of blossom infection.

were involved, but in those whose centers were 22, 44, 66, and 88 feet north of the centers of the northermost trees in the source block, the blossom infection averaged, respectively, 16, 5, 2, and 1 percent. Interestingly enough, all seven gradients observed in the 2 years extended north from the source trees. The spores responsible for this blossom infection must, therefore, have been disseminated by south winds.

The level of disease development varied somewhat among the seven lots of source trees. Such variability resulted from differences in one or more of the following factors: (1) The number of conidia available for dissemination from the source, (2) the number of spores detached from the sporodochia by winds, (3) viability of the conidia, and (4) weather conditions that influence blossom infection. As they stood, therefore, the data were not in a form for comparing disease development between orchards or between years. When, however, the level of disease in each lot of source trees was given equal value, such as 100, and the level of disease in each lot of recipient trees was calculated as a percentage of that at the appropriate source, variabilities resulting from the factors listed above were minimized or eliminated.

The most noticeable result of such a treatment (table 1) was the separation of the data into two groups with respect to the rate that blossom infection diminished with increased distance from the source. The most rapid diminutions occurred in the three gradients observed in 1939, where at 22, 44, 66, and 88 feet from the source tree the blossom infection averaged 39, 21, 12, and 6.5 percent, respectively, of that at the source, as against corresponding values of 55.5, 40.0, 28.0, and 23.0 percent for the four 1940 gradients.

TABLE 1.—*Comparative incidence of blossom infection by Sclerotinia laxa in trees producing sparse inoculum but located at different distances form trees producing an abundance*

Year and orchard	Incidence of disease in recipient trees at stated distances (feet) from the source, expressed as a percentage of the incidence at the source			
	22 feet	44 feet	66 feet	88 feet
1939:				
A	44.4	16.0	9.9	5.1
B	40.1	25.6	11.7	6.3
C	35.1	20.0	13.0	7.7
1940:				
D	56.8	45.1	33.4	26.7
E	55.0	39.0	26.9	19.3
F	45.0	33.3	22.2	19.9
G	61.0	26.8	19.5	15.6
Average,[1] 1939, A to C	39.0	21.0	12.0	6.5
Average,[1] 1940, D to G	55.5	40.0	28.0	23.0

[1] These averages, computed from the original data, are not in all cases equal to the means of the percentages shown above.

Similar infection gradients have been reported for several other fungus diseases, but in comparatively few of these are quantitative data given. Examples of such gradients are furnished by Newhall (*13*) for the spread of onion downy mildew and by Boevsky (*1*) for the spread of wheat leaf rust.

RELATION OF GRADATIONS IN INCIDENCE OF THE DISEASE TO GRADATIONS IN THE DENSITY OF AIR-BORNE SPORES

Unilateral variations in disease development, as illustrated by the cases cited above, suggest that corresponding unilateral variations in the density [5] of air-borne spores existed when the spores were disseminated. Dissemination undoubtedly occurred throughout the late winter and spring, and in various directions from the source trees; but effective dissemination (dissemination resulting in establishment of the disease at different distances northward from the source trees) must have occurred in a period when winds were from the south. According to table 2 the blossoming period in 1939 extended from February 25 to March 17; that in 1940 from February 25 to March 20. Rain fell between March 6 and 9, 1939, when the apricot trees were in full bloom; and between February 25 and February 29, 1940, extending into the early part of bloom. Except for traces of rain the weather was dry throughout the remainder of both periods. Apparently, therefore, most or all of the blossom infection was initiated between March 6 and 9 in 1939 and between February 25 and 29 in 1940. Effective dissemination probably occurred before or during these rains.

Since the recipient trees developing blossom infection were located north of the source trees, the effective conidia must have been disseminated by south winds. Records of wind direction and velocity in the orchards were not available; but, according to weather stations in the districts where the orchards were located, south winds prevailed during the rainy periods of both years (table 2). In both years, furthermore, north winds prevailed for a time immediately before the rains started. Thus, effective dissemination does not seem probable in any part of the blossoming period before infection except during the rainy days (March 6 to 9, 1939; February 25 to 29, 1940).

The Weather Bureau ordinarily records wind movement at some distance from the ground; and, in consequence, the velocity which it reports will exceed that at orchard level. For the writers' purpose, however, the difference in velocitiy between the two periods of spore dissemination is just as important as the exact velocity in the orchard. According to the Sacramento station the average velocity between March 6 and 9, 1939, was 8 miles per hour (table 2), and the average velocity between February 25 and 29, 1940, was 15 miles per hour. During 1940, when the decrease of blossom infection in disease gradients was slow, velocities were 1.88 times greater than in 1939, when the rate of decrease was more rapid. By inference, therefore, the differences in wind velocity account for the observed differences in spore dissemination.

In all probability, the aerial denisty of effective spores was correlated with the unilaterial development of the disease. Boevsky (*1*) demonstrated such a correlation for leaf rust of wheat caused by *Puccinia triticina*. Apparently, however, several factors may alter the quantitative relations between density of spores and level of disease development. By assumption, the amount of blossom infection is proportional to the number of conidia reaching the blossoms; but this proportionality is not necessarily constant. Four factors were

[5] For reasons apparent later, density is definited as the number of air-borne spores that pass through a unit area of a plane perpendicular to the direction of the wind (mean wind direction).

691083—46

TABLE 2.—*Rainfall and wind records during the critical periods for conidial dissemination and blossom infection by Sclerotinia laxa, 1939 and 1940*

Year and data	Month and day																												
	February				March																								
	25	26	27	28	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1939:																															
Blossoming period	←																				→										
Rainfall[1] inches							T			0.11	0.05	1.37	0.68			T	T							T	T						
Average wind velocity (miles per hour)	11.5	15.7	6.5	13.3	7.5	7.5	7.9	6.3	6.2	8.5	8.3	10.4	5.7																		
Wind direction	S N	N	N	N	N	S N	N S	S SW	SE	S SE	S SW	S SE	SE N																		

Year and data	February											March																		
	19	20	21	22	23	24	25	26	27	28	29	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1940:																															
Blossoming period							←																								→
Rainfall[1] inches				0.01	0.06	T	0.88	1.46	2.19	1.01	0.02															T	0.01				
Average wind velocity (miles per hour)	5.5	5.9	5.2	5.5	4.2	5.3	9.6	14.4	20.7	17.6	11.8																				
Wind direction	N NE	N NE	N SE	S SE	N SE	S SE	S SE	S SE	SE	S SW	S SW																				

[1] T=Trace.

mentioned earlier, all of which could affect the relative extent of disease spread between orchards and between years. The effect of these factors on the data in table 1 was minimized by mathematical treatment. There remain other factors that are not affected by this treatment. The first is the possibility that the disease in recipient trees may have been increased by conidia produced on currently infected blossoms. According to Lambert (*9*), in stem rust of wheat the disease zones near barberry bushes, though originating in infection by aeciospores from the bushes, are extended to a much greater degree by urediospores produced on the wheat itself. In brown rot, however, the susceptible period of the host is so short that secondary blossom infection apparently does not occur to any appreciable extent (*20*).

The second factor, illustrated by Boevsky's (*1*) results on leaf rust of wheat, is the tendency for the lesions or comparable foci of infection on recipient hosts nearest the source of spores to become so numerous as to introduce a considerable error in counts of their numbers. This error probably reaches appreciable proportions even before the mechanical difficulties of counting become acute. Since in the present studies the maximum infection in recipient trees nearest the source was only 27 percent of the total blossoms in the trees, there is no reason to suspect that these counts reflect the aerial density of spores less accurately than counts obtained at greater distances from the source.

A third factor is the rain that fell throughout both dissemination periods. Two effects of rain seem possible: (1) Reduction in the number of spores available for dissemination; (2) reduction in the distance the spores are carried by the wind. The first would be caused by rain washing the conidia from the source trees, and the second by rain washing the spores from the air. Effects of variations in the number of spores available for dissemination were minimized by mathematical treatment; but not the effects of rain on the distances to which spores were carried by the wind. While no definite answer concerning the latter effects can be given, rain probably did not cause the observed differences between the 1939 and 1940 disease data, inasmuch as rainfall during the effective dissemination period was heavier in 1940 than in 1939.

On the whole, therefore, the characteristics of the blossom-infection gradients reported in table 1 are believed to have been determined by differences in the aerial density of conidia disseminated from the primary source, the group of nonsprayed trees adjacent to the recipient trees. The remainder of this paper will discuss certain characteristics of aerial dissemination.

EFFECT OF VERTICAL AND LATERAL DISPERSION OF SPORES IN AIR CURRENTS ON THEIR DENSITY AT DIFFERENT DISTANCES FROM THE SOURCE

If, as indicated in the foregoing section, the aerial density of spores is affected by distance from the spore source and possibly by differences in wind velocity, the next feature to examine is the pattern of aerial dissemination. The first question concerns the vertical and lateral dispersion of air-borne spores as they are carried downwind. One need only observe dust or smoke to see that as these materials are blown

from the source the particles are scattered more and more in all directions transverse to the mean direction of the wind. Presumably the cause of this dispersion is the eddies or "turbulence bodies" in the air stream, which are known to be the means for transferring such air properties as temperature, carbon dioxide, and moisture from one point to another in the atmosphere (2, 4).[6] Although turbulence cannot be discussed here in detail, some of its salient features will be mentioned.

According to records made with appropriate meteorological instruments, wind movement is seldom steady for any great length of time, but is marked by recurrent gusts and lulls, associated with cross-current eddies. The eddies vary in duration, but usually last for a few seconds only. Those of shorter duration appear to be distributed at random as regards their movement in directions transverse to the mean direction of the wind. According to Geiger (*4*), the movement of an individual eddy, if it could be followed, would seem fortuitious in the extreme; yet, in the aggregate, the movement of turbulence bodies through a given mass of air accomplishes a transfer of properties in much the same way as molecular diffusion in gases, though at a much greater rate.

The point that bears upon the present problem is the fact that airborne particles, such as the fungus spores acted upon by these eddies, probably tend to "diffuse" or become more and more widely dispersed as they are carried by the wind. Thus, at any given distance from the point at which the spores are liberated into the air, their density will depend upon the number liberated and upon the rate of dispersion. Considering for a moment a source of limited dimensions, such as a sporodochium or fruiting structure of *Sclerotinia laxa*, one sees that if the spores are liberated at successive intervals individually or in clouds, there will be a progressive decrease in the number passing through equal areas of perpendicular planes located at increasing distances from the sporodochium. Whether or not this number bears any constant relation to the distance from the source depends upon whether or not the dispersion of the spores follows a consistent pattern. Probably the simplest relation between distance and spore density would occur if the progressive positions of successive clouds of spores formed sections of a cone whose apex was at the source. Judging from observations on a wind-blown column of smoke, the space dispersion of the particles is roughly conical. If spores behave in this way, their aerial density in plane section would decrease with distance as the area of the right-plane section of the cone increases. Since the area of the right-plane section of all cones increases in proportion to the square of the distance from the apex, spore density, in the sense defined above, would decrease in inverse proportion to the square of the distance. A true conical distribution would occur only if the spores dispersed in such a way that their density was the same at all points in the right-plane sections of the cone and if the right-plane sections were circular. As is shown later, neither of these conditions actually obtains; but no serious error results from assuming an ideal conical space distribution.

The cone, therefore, furnishes a geometric model for studying experimentally the dissemination of spores. Before the experimental results can be described, it is necessary to define certain terms used

[6] The papers pertaining to turbulence in the atmosphere are too numerous to be listed here. Although many were examined by the writers, for the most part the excellent summaries by Brunt (*2*) and Geiger (*4*) were consulted.

in the following discussions. In the representation of a cone in figure 2, let O, the apex, be the source of spores; and let the right-plane sections, I, II, III, be located 5, 10, and 15 feet from the apex. Line P which passes through the "center," C, of each right-plane section is the "projection of the point of release" in the mean wind direction. As the spores are blown downwind they are also dispersed in all directions transverse to P, the "vertical dispersion" of course being above and below the "horizontal dispersion" to the right and left of P. Whenever, in the following discussion, a right-plane section of a cone or any plane perpendicular to the direction of the mean wind is considered, C is called the "center of the plane."

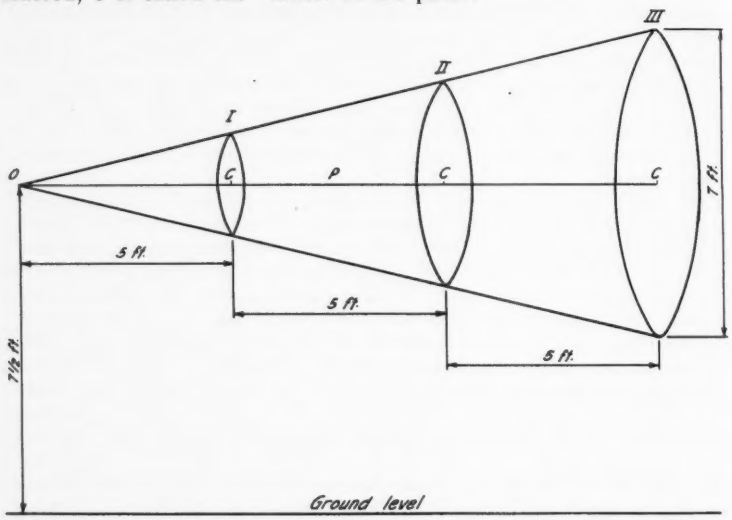

FIGURE 2—Geometric model for studying the relation of the intersecting plane density of air-borne spores to distance from the source.

To determine dispersion of the spores away from the center of the plane, one must determine their density at different points along vertical and horizontal axes of the right-plane sections, I, II, and III. Their array along these axes is termed "distribution," and this term is to be considered in its statistical sense.

DECREASE IN DENSITY OF AIR-BORNE SPORES WITH INCREASED DISTANCE FROM THE SOURCE

To determine the decrease in density of spores at increased distances from the source, a framework was constructed consisting of three slender upright supports (5 feet apart) with cross arms at a distance of 7.5 feet from the ground. On each cross arm were placed five oil-coated slides. Of these, four outlined the circumference of a horizontal cone with its apex 5 feet from the first support and its base on the last support. The fifth slide was placed in the center of the right-plane section of this cone (fig. 2, C). An experimental cone of these dimensions was selected for convenience, not because all the spores were expected to be disseminated within these limits.

Preliminary trials at releasing conidia of *Sclerotinia laxa* proved unsatisfactory because the spores adhered in clumps. It was also difficult to maintain the large supply of spores necessary for frequent tests. Spores of the clubmoss, *Lycopodium* sp., were then tried and found satisfactory. Although these are about 2.5 times greater in diameter than conidia of *S. laxa*, they are readily carried by ordinary air currents. Stepanov (18) reported their rate of fall in still air to be 2.14 cm. sec. They possessed the additional advantages of separating from each other when released into the air and of being easily identified. They can also be obtained in large quantities from commercial sources.

Tests were conducted as follows: The apparatus was oriented with the base of the cone in a downwind direction. A vane anemometer located 7.5 feet from the ground recorded the wind velocity throughout. The spores were released at the apex of the cone (7.5 feet from the ground) by gently expelling them from a small puff-type hand duster, the outlet of which was pointed at right angles to the mean direction of the wind. After successive puffs of spores had been released in this manner for 15 minutes, the slides were removed and examined. To avoid errors—since more spores are ordinarily caught near the edges of the slides than in the center—the same pattern was followed in counting the numbers in 50 microscopic fields on each slide. Inasmuch as the vaseline-cottonseed oil film appeared very uniform, errors arising from differences of adhesiveness between slides are believed to be insignificant.

Table 3 contains the results of 16 tests where the wind varied between 2.2 and 16.0 miles per hour. Since the number of spores released could not be determined with any reliable degree of accuracy, the number caught per given area at the first right section (5 feet from the source) was taken as the reference value which was used to calculate the expected density of spores at 10 to 15 feet from the apex, assuming their density to be the same at all points within sectional limits of the cone. The coefficients for determining the expected density at 10 and 15 feet are 0.25 and 0.111, respectively; that is, at 10 and 15 feet the number of spores per given area should be, respectively, 25 and 11.1 percent of that at 5 feet.

These proportional relations hold for any cone. Although many of the spores were carried outside the limits of the experimental cone, their density varied approximately in inverse proportion to the square of the distance from the source. In some tests the observed value was greater and in some less than the expected value. On the whole, however, the variations appear to be within the limits of experimental error. For various reasons it appears that a closer agreement between the two values might have been obtained had the distances from the source been greater. A material increase in distances between supports, however, would necessitate a framework too long to be easily shifted to meet changing wind directions.

The inverse-square relation between aerial density of spores and distance from the source also holds when but one part of the right section of the cone is considered—that at the center of the plane. Table 4 expresses the relative density of spores on center targets at 10 and 15 feet as a proportion of that on the center target at 5 feet from the source. The observed values vary around their respective

TABLE 3.—*Comparison of the observed and expected density of air-borne spores of Lycopodium at 3 right-plane sections of the experimental cone, observed values are averages of results from 5 targets at each distance*

Wind velocity (miles per hour)	Number of spores on 67 mm.² at stated distances (feet) from source (apex of cone)			
	Data [1]	5 feet	10 feet	15 feet
2.2	Observed	629	230	111
	Expected	629	157	70
2.5	Observed	156	56	19
	Expected	156	39	17
3.5	Observed	170	30	.....
	Expected	170	43	.....
3.8	Observed	484	93	42
	Expected	484	121	54
3.8	Observed	347	158	48
	Expected	347	87	39
4.3	Observed	383	79	39
	Expected	383	96	43
4.4	Observed	591	143	.....
	Expected	591	148	.....
5.1	Observed	809	238	106
	Expected	809	202	90
5.3	Observed	550	168	58
	Expected	550	138	61
5.6	Observed	446	145	66
	Expected	446	112	50
8.5	Observed	1,396	361	165
	Expected	1,396	349	155
11.3	Observed	1,340	307	115
	Expected	1,340	335	149
12.1	Observed	478	130	.....
	Expected	478	120	.....
12.5	Observed	608	145	.....
	Expected	608	152	.....
12.5	Observed	618	145	.....
	Expected	618	154	.....
16.0	Observed	2,764	779	326
	Expected	2,764	691	307
Average	Observed	736	200	100
	Expected	736	184	94

[1] Expectancy at 10 feet is 25 percent and at 15 feet 11.1 precent of that at 5 feet.

TABLE 4.—*Density of air-borne spores of Lycopodium in a direct line 10 and 15 feet to windward of the point of release, values expressed as percentages of the density at 5 feet from the point of release*

Wind velocity (miles per hour)	Number of tests averaged	Number of spores caught at stated distances (feet) for each 100 spores caught at 5 feet	
		10 feet	15 feet
2.0–2.5	2	34	10
3.1–3.8	3	32	11
4.1–4.4	3	25	11
5.1–5.9	4	26	12
6.6	1	22	7
8.1–8.5	2	31	14
11.3	1	24	10
12.1–12.5	3	25	10
13.4	1	29	13
16.0	1	32	12
Mean of 21 tests		28	11
Expected if dispersion is concial		25	11

means, which in turn are close to the theoretical values. Again the agreement between observed and theoretical is closest at the greater distance from the source of spores.

Heald, Gardner, and Studhalter (*6*), working with *Endothia parasitica*, and Lambert (*9*), working with *Puccinia graminis*, found the number of air-borne spores to decrease rapidly as distance from the source increased. Stepanov (*18*) studied the dissemination of *Tilletia tritici* and *Bovista plumbea* by releasing the spores at a given point 0.5 to 3 meters above the ground and catching them on glass slides placed face up on the ground at various distances downwind from the point of release. In three tests when wind velocity varied between 5 and 6 m. p. h. the numbers of spores caught at 10, 15, 20, and 40 m. were 24.1, 11.9, 7.99, and 1.2 percent respectively of the number caught at 5 m. When dissemination follows a conical pattern, the expected percentages should be 25.0, 11.1, 6.2, and 1.6 respectively. Boevsky (*1*) studied the dissemination of urediospores of *Puccinia triticina* from a field of winter wheat. His data are complicated by two facts: (1) The urediospores of *P. dispersa* from a nearby rye field were included in the counts at certain times; (2) the spring wheat surrounding the spore traps became infected by *P. triticina* and produced urediospores. If one omits from Boevsky's data the counts in which these complications occurred, the numbers of spores caught at 50, 100, and 200 meters from the edge of the source field were 322, 119, and 27 respectively, whereas the numbers expected when dispersion is conical should be 322, 80, and 20.

DISTRIBUTION OF AIR-BORNE SPORES IN THE VERTICAL DIRECTION TRANSVERSE TO THE MEAN WIND DIRECTION

Despite the concordance between experimentally observed results on spore density and the results expected if dispersion were conical, the distribution of spores within the cross-sectional area of the cone was not uniform. Their density was greatest at the center of the plane—that is, at the level of release—and decreased outward to the periphery of the experimental cone and beyond. Since the number of targets at each right-plane section was insufficient for showing the over-all vertical distributions of the spores the experimental apparatus was redesigned. Beginning 18 inches from the ground, 13 slides were placed at 1-foot intervals on each of the three vertical supports, which (as will be remembered) were 5 feet apart. Tests were conducted as follows: After the apparatus had been oriented to the direction of the mean wind, the spores were released at a point 5 feet from the first vertical support and at a height of 7.5 feet; that is, on the level with the center slide in each vertical series.

Table 5 gives results of the tests conducted at seven different wind velocities. The array of spores above and below the center of the plane was roughly similar. In gross aspects the distributions followed that of normal probability. In a given test the vertical distributions occurring at 5, 10, and 15 feet from the source differed noticeably; the dispersion of spores increased with distance. A measure of dispersion is afforded by the standard deviation of the distributions. The distributions obtained at all three distances in winds blowing 5.9 to 16.0 miles per hour and those obtained at 5 feet in winds blowing 3.8

TABLE 5.—*Vertical distributions of air-borne spores of Lycopodium at successive distances from the point at which the spores were released; standard deviations express the degree of dispersion at the stated distances*

Distance, in feet, above (+) and below (−) level at which spores were released	Number of spores on 67-mm.² area at stated wind velocity and at stated distances (in feet) from the source of spores																				
	3.8 m. p. h.			5.9 m. p. h.			6.4 m. p. h.			8.1 m. p. h.			8.5 m. p. h.			13.4 m. p. h.			16.0 m. p. h.		
	5	10	15 [1]	5	10	15	5	10	15	5	10	15	5	10	15	5	10	15	5	10	15
+6	3	3	15	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	2
+5	2	9	16	0	0	9	0	0	0	0	0	1	0	0	5	0	0	11	0	1	10
+4	5	13	5	0	8	17	0	0	3	0	1	6	0	1	9	0	4	14	1	3	16
+3	7	35	12	0	7	31	0	3	8	1	6	30	0	18	34	1	13	39	1	32	63
+2	16	14	14	8	34	27	5	18	17	10	35	58	14	55	50	41	27	49	25	143	94
+1	97	36	18	183	144	60	83	60	26	133	118	73	214	138	62	170	92	70	619	284	139
0	172	97	27	932	206	104	317	64	25	632	250	106	941	228	105	716	210	94	1,446	457	167
−1	80	77	12	87	108	65	34	41	27	328	157	81	241	125	79	241	158	81	699	277	152
−2	48	40	15	6	24	23	1	7	13	33	79	59	18	54	44	11	61	51	44	137	97
−3	17	15	13	1	3	16	0	1	3	1	19	31	0	15	11	1	5	19	2	49	48
−4	17	5	12	0	0	2	0	0	2	0	2	7	0	1	3	0	0	7	0	6	4
−5	4	3	9	0	0	5	0	0	0	0	0	1	0	1	4	0	0	1	0	0	0
−6	1	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mean (in feet) measured from the level of release (below—minus)	−0.26	0.10	2.90	0.08	0.19	0.35	0.13	0.24	0.21	−0.21	−0.25	−0.02	−0.02	0.03	0.26	−0.01	−0.16	0.28	−0.04	−0.02	0.16
Standard deviation (σ) in feet	1.64	2.10	5.95	.52	1.13	1.95	.55	1.08	1.67	.73	1.20	1.80	.64	1.29	1.84	.73	1.20	1.96	.76	1.37	1.85

[1] This distribution is obviously incomplete and hence the estimation of the mean and standard deviation present technical difficulties. The estimates given here are obtained by applying the method of difference equation graduation for a stump of a normal distribution curve as explained by Carver (3).

miles per hour were considered to be complete, and the means and standard deviations were obtained in the usual manner. For the incomplete distributions at 10 and 15 feet in the 3.8 miles per hour wind, however, these statistics had to be determined by difference-equation graduation, as explained by Carver (*3*). The analyses also appear in table 5.

Several features of these data should be discussed: (1) Even at the lowest wind velocity *Lycopodium* spores, which are heavier than the conidia of *Sclerotinia laxa*, were carried upward for several feet within a comparatively short horizontal distance from the source; (2) judging from the standard deviations, vertical dispersion of the spores increased approximately in proportion to the distance from the source; (3) though the means increase slightly between 5 and 15 feet, on the whole the spore dispersion in a vertical direction occurred at random.

According to Schmidt (*17*) the air-borne distribution of very light seeds and of spores is normal (in a statistical sense). This conclusion follows from an analogy with the transfer of heat outward from its source. The observed distributions in table 5 partially confirm Schmidt's statement: they can be described in their gross aspects, as normal; yet, since they are rough or knobby, they cannot be regarded as coming from a normal distribution by means of random sampling alone. There is a plausible explanation: the eddies in the air move as comparatively large bodies, not as small particles. These turbulence bodies, carrying different numbers of spores and maintaining their identity for considerable periods before mixing with the surrounding air, may cause momentarily large variations in the density of spores between adjacent small areas of air. Thus in experiments such as these where the spores were released for a relatively short time, some unevenness in distributions must be expected. Extending the period of release should usually result in smoother distributions. This point will be noted again in the following section.

Mention of the size of turbulence bodies raises a question regarding the effect of tree branches on the distributions. Air movement through the orchard (without leaves, as during the blossoming period) should be more turbulent than air moving over the open ground, as in the foregoing tests. To some extent, probably, the branches would reduce the size of turbulence bodies; but in any event the mixing of the air should be increased over that occurring in the open. To determine how the tree branches affect vertical distribution of *Lycopodium* spores, four tests were conducted during the winter when trees were not in leaf. First, the spores were released over open ground and were caught 15 feet from the point of release; then the apparatus was quickly transferred to a small orchard, and the spores were so released that they were carried through the branches of one tree before being caught on the vertical series of slides 15 feet away. In all cases the air currents moved through the branches of four trees before reaching the point of release. This is mentioned because the turbulence of the air probably would increase as it passed through the limbs of more and more trees. According to table 6, the spores became more widely dispersed within the orchard than over open ground. Apparently, therefore, the vertical component of turbulence is greater in the orchard than in the open. Presumably the same would be true of the horizontal component.

The trees have an effect on wind velocity. Data on this feature are comparable, since the average wind velocity over open ground was found to vary little during the time each pair of tests (outside and inside the orchard) was conducted. The trees always reduced wind velocity, but apparently the reduction was least at the lowest velocity. When , for example, the velocities in the open were 4.9 6.6, and 8.7 m. p. h., the velocities in the orchard decreased, respectively, 0.9, 2.1, and 3.4 m. p. h. Apparently, therefore, trees not only impede the movement of air currents but somewhat lessen the range of velocities.

TABLE 6.—*Effect of dormant orchard trees on wind velocity and on vertical dispersion of air-borne spores of Lycopodium*

Date	In open		In orchard [1]	
	Wind velocity	Standard deviation of distribution [2]	Wind velocity	Standard deviation of distribution [2]
1944	*M. p. h.*		*M. p. h.*	
Feb. 4	4.9	1.31	4.0	2.31
Jan. 27	6.6	1.78	4.5	1.99
Feb. 15	8.7	1.97	5.3	2.05

[1] A small orchard of dormant trees. In all cases the wind moved across 4 rows of trees before reaching the area where tests were conducted.
[2] Vertical distribution 15 feet from point at which spores were released. In the orchard the spores were released on one side of a tree and caught 15 feet away on the other side.

DISTRIBUTION OF AIR-BORNE SPORES IN THE HORIZONTAL DIRECTION TRANSVERSE TO THE MEAN WIND DIRECTION

Tracing made by means of the bidirectional wind vane show that the amplitude of the horizontal variations of eddies is greater than that of the vertical variations near the earth's surface. At a height of 2 m., for example, the ratio of the horizontal to vertical amplitudes (h/v) is 1.59. This ratio decreases to 1.2 at 18 m. and is probably 1.0 at somewhat greater heights (*2*). To ascertain the dispserion of spores in the horizontal direction, transverse to the direction of the mean wind, cross arms were attached (at a height of 7.5 feet) to the apparatus described earlier. Distribution of spores could then be determined for a distance of 6 feet to the right and left of the vertical support, as well as 6 feet above and below the horizontal cross arm.

Table 7 gives the results from four tests conducted at wind velocities of 3.8, 6.1, 7.2, and 10.3 miles per hour. On the whole, distribution in the horizontal direction followed that of normal probability; but difficulties were encountered in orienting the apparatus with the true direction of the mean wind. Sometimes, therefore, the peak of spore density occurred to the right or left of the center of the apparatus. When spores were released for a relatively short time, say 15 to 20 minutes, the distributions proved to be somewhat rough and knobby. The explanation, apparently, was that the shifts or variations in the horizontal direction are of fairly long duration as compared with those in the vertical direction. A common characteristic of horizontal variation seems to be progressive rather than instantaneous shifts to one side or the other, then progressive shifts in the opposite direction. As a result, clouds of spores released in rapid succession would be

carried to the right or left of the mean direction for several seconds before they are again carried the other way. When the period of release was increased to 30 minutes or more, the resulting distributions were found to resemble more nearly that of normal probability.

TABLE 7.—*Comparison of the vertical and horizontal dispersion of air-borne spores of Lycopodium as measured by the standard deviations of corresponding distributions above and below and to the right and left of the projection of the point of release*

Wind velocity (miles per hour) and dimension	Standard deviations (σ) of distributions at stated distance from point of spore release		σ 15 ft./ σ 5 ft.	σ h/σ v	
	5 feet	15 feet		5 feet	15 feet
3.8:					
Vertical	0.62	1.59	2.56	1.74	1.56
Horizontal	1.08	2.48	2.20		
6.1:					
Vertical	.61	1.81	2.97	2.41	1.32
Horizontal	1.47	2.39	1.63		
7.2:					
Vertical	.59	1.55	2.63	1.59	1.49
Horizontal	.94	2.32	2.47		
10.3:					
Vertical	.55	1.53	2.78	1.96	1.84
Horizontal	1.08	2.81	2.60		

The outstanding feature of the results in table 7 is the consistency with which the standard deviations of horizontal distributions exceed those of vertical distributions. At 5 feet from the point of release the ratio $\sigma h/\sigma v$ averaged 1.93, and at 15 feet it averaged 1.55. The latter is very close to the ratio 1.59 obtained by means of tracings made with the bidirectional wind vane at 2 m. (6.56 feet) from the ground (*2*).

At 5 feet from the point of release the standard deviations of horizontal distributions averaged 1.14, at 15 feet 2.5, a ratio $\frac{(\sigma \text{ 15 feet})}{(\sigma \text{ 5 feet})}$ of 2.19. The corresponding values for vertical distribution are 0.59 and 1.62, and the ratio is 2.74. Thus the dispersion of spores in both dimensions increased roughly in proportion to distance from the source. Whether the difference between the two ratios indicates that the rate of dispersion in the vertical was somewhat greater than that in the horizontal was not apparent from the data. These results will be discussed again later in relation to wind velocity.

Whether the conidia of *Sclerotinia laxa* are released into the air singly, in continuous streams, or intermittently in clouds as in the foregoing tests, probably makes little difference in the manner in which they are dispersed vertically and horizontally. When dispersion is measured in a plane perpendicular to the mean wind direction, the distribution resulting from numerous small clouds having passed through the plane resembles the distribution that would result from dispersion of individual spores in a plane through the center of a single cloud of spores moving in the direction of the mean wind. That is, spore density is greatest at the center of the plane and decreases toward the periphery. As the cloud moves farther from the source it continually expands because spores are continuously dispersed vertically and horizontally. Hence the geometrical model that best

describes the expansion of this hypothetical cloud of spores is a cone. We have just seen, however, that this cone is not circular in cross section, but is greater in the horizontal dimension. As noted earlier, though ideal conical distribution of spores does not occur in nature, the density of spores in a plane perpendicular to the projection of the apex (the point of release) varies approximately in inverse proportion to the square of the distance from the source.

According to Brunt (*2*), eddies of short life apparently occur at random with respect to their movement transverse to the main air current. This supposition seems to be borne out by the manner in which spores are dispersed. In order to visualize more clearly the effect of turbulence on dispersion of air-borne material, the following experiment was devised. A single vertical support bearing a cross arm 4.5 feet from the ground was constructed. Each of the vertical and horizontal arms was plainly marked at 1-foot intervals. After

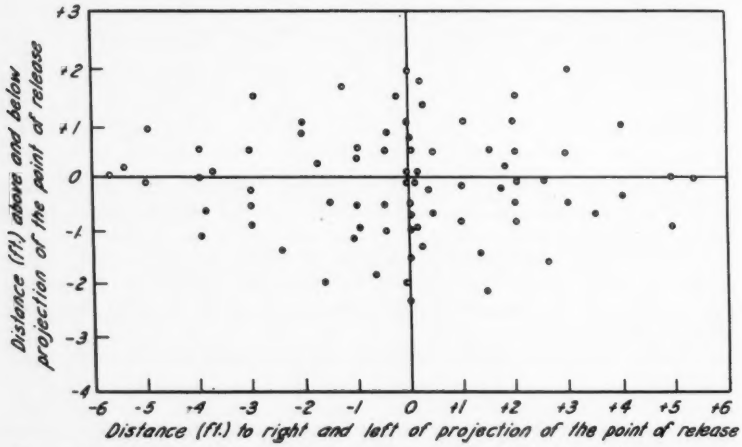
+3
+2
+1
0
-1
-2
-3
-4
Distance (ft.) above and below projection of the point of release
-6 -5 -4 -3 -2 -1 0 +1 +2 +3 +4 +5 +6
Distance (ft.) to right and left of projection of the point of release

FIGURE 3.—The dispersion of "smoke" clouds by eddies in the wind. Smoke formed by aspirating fumes of ammonium hydroxide through hydrochloric acid was released from a position 4.5 feet above the ground and 16 feet from the supports. Wind velocity 6.4 miles per hour.

orienting the structure to the direction of the mean wind, small puffs of "smoke" formed by aspirating fumes of ammonium hydroxide through hydrochloric acid were released in rapid succession from a position 16 feet from the supports and 4.5 feet from the ground. As the smoke clouds passed the support, the position of their centers relative to the vertical and horizontal markings was noted, and thus data were secured from which to construct the kind of diagrams illustrated by figure 3. Though these tests were not numerous, all showed that dispersion of the individual smoke clouds was greatest at the horizontal position and decreased to a minimum at the vertical. The outline of the diagram, in consequence, was roughly oval. Though the smoke particles may not behave in the same manner as spores, the tests showed how the clouds are partitioned approximately equally between the quadrants of the oval—although, in the tests illustrated,

there was some tendency for more clouds to be carried below than above the horizontal axis, possibly because the particles were heavy enough to be influenced by gravity. What the diagram does not show is the dispersion of the particles in the individual clouds which, upon being carried downwind, rapidly expanded and reached the point of invisibility shortly after passing the support.

It is interesting to compare the horizontal and vertical dispersion of these smoke clouds with tracings obtained by means of bidirectional wind vane. The standard deviation of the horizontal dispersion (σ h) in figure 3 is 2.46, that of the vertical dispersion (σ v) is 0.98, and the σ h/ σ v ratio is 2.5. With the wind vane, tests (*2*) at a height of 2 feet gave an h/v ratio of 3 and at 8 feet 1.4. Interpolating to 4.5 feet, the height of the smoke tests, we obtain 2.0, a figure not far from our value.

RELATION OF WIND VELOCITY TO DISPERSION OF AIR-BORNE SPORES TRANSVERSE TO THE MEAN WIND DIRECTION

Assuming for the moment that higher wind velocity explains why the incidence of disease decreased less rapidly with distance in 1940 than in 1939, the question is how can velocity be correlated with density of air-borne spores. One possibility would be that the spores were subject to less dispersion per unit of distance from the source in high winds than in low winds. For a given number of spores released at the source, the less the dispersion per unit of distance traveled from the source, the greater the total number carried through the recipient trees during the period of effective dissemination. We are speaking here of the total numbers of spores reaching equal areas in the recipient trees at different distances from the source, and not of the rate at which these numbers decrease, for, in the experimental results presented earlier, the density of air-borne spores decreased at the same rate at all wind velocities between 2 and 16 miles per hour. Since the spore dispersion follows an approximate conical pattern, and since in the experiments relating to spore density the samples collected by means of oil-coated slides were uniformly scattered over right sections of cones at different distances from the apex, then for each apex distance we were dealing with a constant proportion of the total number of spores liberated. This is so because the area of the cone base is proportional to the square of the distance from the apex. Besides, as shown earlier, the standard deviations of spore distributions, which express the degrees of dispersion, are also proportional to the distance from the apex; hence the area of the right section is proportional to the square of the standard deviation. When the ratio of the number of spores per unit area (density) is taken for two different distances, the total number of spores and the constant proportion of this total number, which depend upon the degree of dispersion, cancel out. The result; that is, the rate of changes in density—is then independent of the degree of dispersion, and therefore of any effect that wind velocity might have on dispersion.

If, on the other hand, the rate at which the spores disperse as they are blown downwind is altered, the rate at which their density decreases from one distance to another will not change; but the total number of spores passing through a given area of a vertical plane will. A decrease in dispersion rate can be visualized as a contraction in the

diameter of the hypothetical cone of dispersion. Thus, with a given number of spores liberated at the source, the more the cone contracts the greater is the number of these bodies passing through a unit area of its right sections.

Effects of wind velocity must be looked for, accordingly, in the data on spore dispersion, not in the data on comparative densities. Aside from somewhat larger standard deviations for distributions at 3.8 miles per hour, the values pertaining to dispersion in table 5 change little if any with changes in wind velocity. Those in table 6 increased somewhat, whereas those pertaining to vertical dispersion in table 7 decreased slightly. In another series of 26 tests, vertical dispersion was determined at 5 feet from the source. The mean values presented in table 8 indicate that dispersion was high at low velocities but varied little between medium and high velocities. These data and those in table 5 are open to two interpretations: (1) The degree of dispersion decreases rapidly between low velocities, but much less rapidly between medium and high ones; (2) if velocities (5 miles per hour or lower) at which winds are notably variable in direction are disregarded, the degree of dispersion at equivalent distances displays no significant tendency to change with wind velocity.

TABLE 8.—*Standard deviations of vertical distributions of air-borne spores of Lycopodium 5 feet from the source at various wind velocities*

Wind velocity (miles per hour)	Mean standard deviations (σ) of vertical distributions	Wind velocity (miles per hour)	Mean standard deviations (σ) of vertical distributions
1–3	1.57	9–11	.45
3–5	1.13	13–15	.62
5–7	.58	15–17	.59
7–9	.64	17–19	.45

Presumably dispersion would be affected by changes in the turbulence of the air. At the height at which these tests were conducted (7.5 feet) the main source of turbulence is friction along the earth's surface (*15*). A second source, thermal, is afforded by a decrease in air temperature with height above the earth. If this decrease is greater than the adiabatic lapse rate, warm air will tend to rise. On the whole, thermal turbulence is most pronounced at low wind velocity. Even moderate air flow prevents the formation of a steep temperature gradient and thus is unfavorable for thermal turbulence. Frictional turbulence, on the other hand, increases with increased air flow. Gustiness of the wind, and consequently the strength of cross eddies, is said (*15*) to be about proportional to wind velocity. Judging from measurements made with the bidirectional wind vane, the ratio of vertical to downwind velocities in eddies increases with wind velocity, but the ratio of the horizontal to downwind velocities is less noticeably affected (*2*). The ability of strong winds to lift and carry dusts to great heights is widely recognized. Apparently less is known, however, about the effects of variations in wind velocity on the rate at which wind-borne material is elevated in comparison with the rate at which it is carried downwind. Consider, for example, the situation illustrated by figure 4. Assume that dispersion at a distance

x for an 8 miles per hour wind is 1. Assume also that as wind velocity increases the rate of turbulence increases, but somewhat more slowly than that of wind movement. If an 8 miles per hour wind moves a distance x in t time, a 16 miles per hour wind would move the distance x in $\frac{1}{2}$ t time or 2 x distance in t time. In table 5 we can compare the standard deviation (0.73) of dispersion at 5 feet from the source for an 8.1 miles per hour wind with that (1.37) at 10 feet from the source for a 16 miles per hour wind; when velocity doubles the degree of dispersion increased 1.9 times.

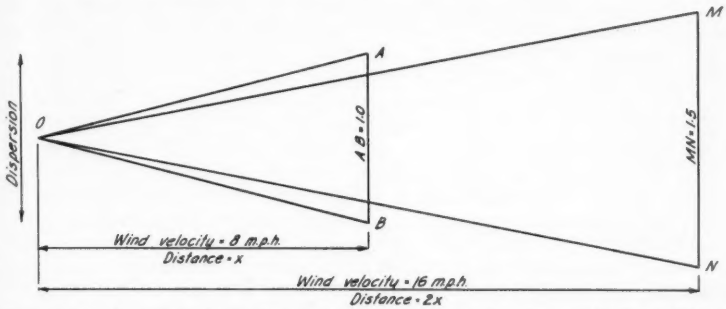

FIGURE 4.—A comparison of the relations between the degree of dispersion of air-borne spores at a given distance, x, from the source of spores when the rates of increase in dispersion and wind velocity are 1.5 and 2, respectively.

However, to show wind-velocity effects in figure 4 the degree of dispersion for a 16-mile-per-hour wind is assumed to be 1.5 at 2 x distance. Representing the dispersion in an 8-mile-per-hour wind by bar AB at x distance from the source O, and dispersion in a 16-mile-per-hour wind by bar MN at 2 x distance, if dispersion is conical; that is, if it increases in proportion to the distance from the source, as indicated by the experimental results—the degree of dispersion at all distances from the source will be represented by lines OA and OB for an 8-mile-per-hour wind, and by lines OM and ON for a 16-mile-per-hour wind. In this situation, as inspection reveals, the degree to which the spores are dispersed at x distance by a 16-mile-per-hour wind is less than that for an 8-mile-per-hour wind. At a given distance, therefore, the degree of dispersion will diminish as wind velocity rises, unless the increase in the rate at which the spores are dispersed equals or exceeds the increase in the rate at which they are carried downwind.

With these relations in mind we shall reexamine the spore-dissemination results. At low-wind velocities dispersion was frequently much greater than at medium velocities; but it did not diminish noticeably throughout medium and high ranges (tables 5 and 8). Many of these tests were conducted on sunny days when conditions favored thermal turbulence. This type of turbulence probably played a considerable part in vertical dispersion, especially when wind movement was low. Moreover, because winds of low velocity are noticeably variable in direction, the spores would probably be much more widely scattered at such velocities than at higher ones. For these reasons, we are not fully warranted in attributing the rapid decrease in dispersion between low and medium velocities to the diminishing effects of

frictional turbulence. If results obtained at velocities below 5 miles per hour are excluded, the standard deviations obtained for medium and high velocities are found to exhibit no consistent variations. For example, none of the values for velocities above 3.8 miles per hour in table 5 show marked differences, especially if corresponding standard deviations for 5.9 and 6.4 miles per hour and those for 8.1 and 8.5 miles per hour are averaged. Likewise, the values for velocities above 5 miles per hour in table 8 show little tendency to vary with wind velocity. If, therefore, the interpretation regarding the relation of dispersion to distance, as given in figure 4, is correct, these results indicate that dispersion increases at approximately the same rate as wind velocity for distances up to 15 feet. The standard deviations in table 6, column 3, indicate, on the other hand, that the rate of dispersion increased about 1.37 times faster than wind velocity, whereas the values pertaining to vertical dispersion in table 7 indicate the rate of increase to be about 0.85 times that of the increase in wind velocity. Thus the average value for all four series is approximately 1—a unit change in velocity resulted in a unit change in vertical dispersion.

About horizontal dispersion much less is known. Judging from the results reported for the bidirectional wind vane (*2*), turbulence in this dimension changes little if any as wind velocity increases. If such is the case, we should expect from the analysis in figure 4 that standard deviations of horizontal distribution at 5 and 15 feet in table 7 would decrease as velocity increased from 3.8 to 10.3 miles per hour. There is a suggestion of a decrease; but, as noted earlier, considerable difficulty was encountered in determining over-all distribution in the horizontal, and so the results do not justify conclusions.

Turning to the results on spread of the disease in apricot orchards (table 1), we find the incidence of blossom infection between the source and the fourth row of recipient trees (88 feet) to have decreased 94.5 percent in 1939 and 77 percent in 1940, a difference of 17.5 percent. Presumably, therefore, the density of spores varied to a similar degree. A difference of 17.5 percent in dispersion at 88 feet from the source probably represents a much smaller difference in density. In any event, these results may be explained as due to the differences between wind velocities at the two effective dissemination periods, provided the rate at which the spores were dispersed relative to the rate they were carried downwind is assumed to have been less in 1940 than in 1939. In some of the tests mentioned above, the ratio of change in wind velocity to change in vertical dispersion was 1.0 : 0.85; but this may have been due to chance, because in other tests the ratio was 1.0 : 1.37 and the average of all tests was approximately 1.0 : 1.0. If increases in horizontal dispersion did not keep pace with increases in wind velocity, the aerial density of the spores would diminish as wind movement increased in cases where the source of spores is a limited area. When, however, the source extends an appreciable distance transverse to the wind direction, such as a block of trees may do, dispersion in the horizontal would probably not be greatly affected. Apparently, therefore, the assumption above will be valid only if the rate of vertical dispersion increases somewhat more slowly than that of wind velocity.

INTERCEPTION OF SPORES BY THE TREES AS A FACTOR IN AERIAL DENSITY AT INCREASING DISTANCES FROM THE SOURCE

What effect does the interception of air-borne spores by the trees have on the density of these bodies? This discussion was purposely delayed until all experimental data had been presented. More specifically the question is, will the number of spores caught by the trees significantly diminish the density at subsequent distances, and might the number caught vary with wind velocity?

That such a loss reduces the aerial density cannot be denied. As will be recalled, however, in the experimental work the glass slides caught large numbers and yet their aerial density did not consistently diminish more rapidly than was to be expected from conical dispersion. In these tests, moreover, the decrease in density was not affected by variation in wind velocity. The number of spores caught on branches and blossoms may have affected the incidence of disease in recipient trees, but how greatly cannot be estimated.

MATHEMATICAL MODEL OF DISPERSION IN WIND-BORNE SPORES

Despite some conflicting results reported in the previous sections, certain features seem to be clearly established. We shall list them. 1. The average wind velocity in 1940 was 1.88 times greater than that of 1939 during the respective periods of effective spore dissemination. 2. The horizontal and vertical distributions of spores were approximately normal. 3. The results obtained in the open are not directly applicable to orchard conditions; for instance, the wind velocity is reduced 18, 32, and 37 percent for velocities of 4.9, 6.6, and 8.7 miles per hour (table 6), and the limbs have a pronounced effect on turbulence. 4. The standard deviations of the vertical and horizontal spore distributions increase with distance from the source. 5. The infection gradients were very different in the 2 years 1939 and 1940. It is not definitely established that wind velocity affected the standard deviations of the spore distribution at equivalent distances from the source. Certain of the experimental data suggests, however, that this might be the case under some conditions.

We shall construct a mathematical model of wind-borne spore dispersion that conforms to the clearly established facts. Some gaps will have to be bridged. If further investigations show that this bridging has not been done properly, then the model can be modified to take account of the new data.

First let us observe that the data of figure 5 can be very well represented by the equations

$$y=\frac{1{,}938}{x^{1.2362}} \tag{1}$$

for the year 1939 and

$$y=\frac{551.8}{x^{0.7123}} \tag{2}$$

for the year 1940, where y is the percent of infection in successive rows of recipient trees in terms of the percent of infection in the source trees and x is the distance of the centers of successive recipient

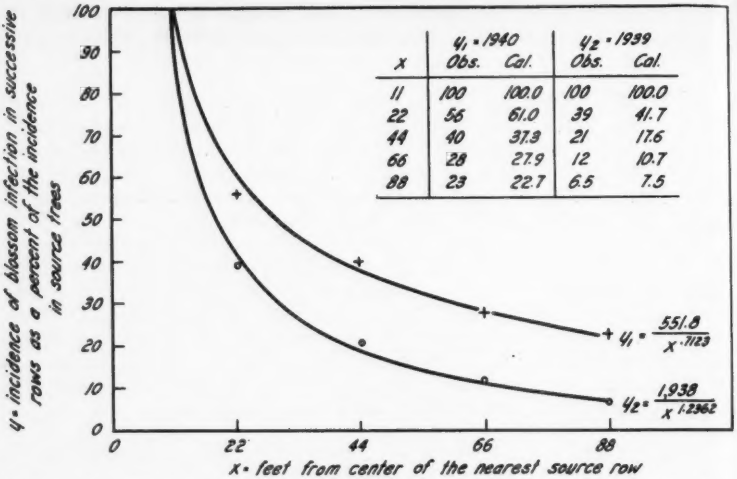
y • incidence of blossom infection in successive rows as a percent of the incidence in source trees
x • feet from center of the nearest source row
y1 • 1940
y2 • 1939
x | Obs. Cal. | Obs. Cal.
11 | 100 100.0 | 100 100.0
22 | 56 61.0 | 39 41.7
44 | 40 37.9 | 21 17.6
66 | 28 27.9 | 12 10.7
88 | 23 22.7 | 6.5 7.5
y1 = 551.8 / x^.7123
y2 = 1,938 / x^1.2962

FIGURE 5.—The relative incidence of blossom infection by *Sclerotinia laxa* in apricot trees at various distances from the source of conidial inoculum, and at mean wind velocities of 15 miles per hour (+) in 1940 and 8 miles per hour (°) in 1939. The curves were fitted by means of equations developed from a theoretical treatment of spore distributions given in the following section.

rows from the center of the first row of the source trees—that is, x takes the values 22, 44, 66, 88 for the successive recipient rows (table 1). These formulas[7] were obtained by making an equation of the form

$$y_i = \frac{A}{x^p} \tag{3}$$

pass through the point with an abscissa of 11 and an ordinate of 100, and then averaging the observational equations to obtain the value of log A. The abscissa value of 11 feet seems to be indicated for the following reason: Since the branches of the trees extended approximately halfway between rows, the area from which the spores were supplied did not end at the center (trunks) of source trees that were nearest the first row of recipient trees. A distance halfway (11 feet) between the last source row and the first recipient row, therefore, was chosen as the place at which a decrease in the aerial density of the conidia began. Choosing this point for the beginning of decrease in infection permits very good representations of the observed data as shown in figure 5.

Let us now begin at the beginning of spore dispersion and see what is necessary to arrive at the result expressed by equation 3. According to Brunt (*2*), who was reporting the work of others, the

[7] An article by P. H. Gregory (*5*) was published in the Transactions of the British Mycological Society after the present paper was submitted for publication. To describe the pattern of spore dispersion Gregory employs an equation developed by meteorologists from studies of the transfer of heat, momentum, and matter by eddy diffusion. In general, this equation and equation 3 of the present paper give similar results, the major difference being in the range of the exponent for distance, x.

standard deviations of horizontal and vertical distributions of smoke particles, dye in water, and the like are of the form

$$\sigma = ax^p \tag{4}$$

Here σ is the standard deviation of a distribution at a distance x from the source, a is a constant, and p is a number between ½ and 1; and the horizontal distributions are independent of the vertical distributions.

In view of the investigations carried out by others (*8*) as well as those cited in this paper we shall assume that

$$\sigma_{vx} = ax^p, \ \sigma_{hx} = bx^q \tag{5}$$

Here σ_{vx} and σ_{hx} are respectively the standard deviations of vertical and horizontal spore distributions at distance x from the source; a, b, p, and q are quantities that may depend on wind velocity but do not depend on x; and the horizontal and vertical distributions are normal and independent of each other. We shall admit values from ½ to 2 for p and q, instead of ½ to 1 as other investigators have suggested. We must assume that p, q, a, and b depend on wind velocity, in order to account for the observed difference between infection gradients for the 2 years 1939 and 1940. Separate representations are used for σ_{vx} and σ_{hx} because, as shown in the previous discussions, the vertical and horizontal distributions behave somewhat differently.

On the basis of these assumptions and the consideration of a block of sources, we are led to equation 3 as a valid approximation of the infection gradient if x is sufficiently large.

If we plot our two values of p given in equations 1 and 2 against wind velocity and extrapolate back to zero wind velocity, we get 1.81 for p. This is fairly close to 2.0, the value of p corresponding to the relation between y and x for a conical distribution. Judging from the present data, p may lie between 0.5 and 2.0. We are now considering a block source, not a point source as in the experiments described in the earlier sections.

The percentages of infection, furthermore, depend only on the standard deviations of the vertical distributions.

In conclusion, let us make three assumptions—(1) the percent of infection is proportional to the number of spores reaching a given area; (2) the general level of blossom susceptibility is measured by the percent of blossom infection in the source trees; (3) spores fan out from a single source in such a way that both horizontal and vertical distributions are normal and independent, with standard deviations proportional to some power of the distance from the source (not necessarily the same) and with means that lie on the line of projection of the source in the average direction of the wind. Then the ratio, y, of the percent of infection in a vertical slice of susceptible blossoms at a perpendicular distance x from the source plane to the percent of infection in the source trees is given to a good first approximation by an equation of the form

$$y = \frac{A}{x^p}.$$

Here A and p are constants that depend on average wind velocity and perhaps, to a lesser extent, on many other quantities; and x is

measured from the center of the first row of source trees. The assumptions stated above have been made plausible by data collected in specially designed experiments and by a wide survey of the existing literature. Two distinct sets of data have been successfully treated on the basis of these assumptions (fig. 5).

DISCUSSION

Many details concerning the aerial dissemination of spores and the spread of the disease that the spores incite must be studied before general conclusions are warranted. Further study of certain details, however, must await an improvement in the method for measuring dispersion, since the method for ascertaining the over-all distribution of spores at intercepting planes is not adapted to greater distances than those employed herein. Additional studies should include, among other things, a comparison of dissemination over open ground with that through orchard trees.

Since the zone of frictional turbulence in the atmosphere is limited in depth and since the magnitude of its vertical component varies with height, the pattern of spore dispersion aloft might well differ from that near the earth's surface. Judging from results by Durham (*12*), spores carried into the upper air may at times reach a "ceiling" above which they are not readily dispersed. Such a ceiling might well occur at the lower boundary of an inversion in the upper atmosphere. According to Lyman (*10*), the smoke from certain forest fires remained in the air at a density sufficient to affect visibility for hundreds of miles southeastward. Points regarding the long-distance transportation of spores in air masses are discussed by Durham (*12*), Lambert (*9*), Rittenberg (*16*), ZoBell (*12*), and Jacobs (*7*).

SUMMARY AND CONCLUSIONS

Conidia of *Sclerotinia laxa*, the cause of a blossom blighting of stone-fruit trees, are produced in large numbers during late winter on blossoms and twigs that were blighted the previous spring. These are detached from the sporophores by winds of low velocity and, judging from their rate of fall in still air, are readily transported by air currents.

Spread of the disease through apricot orchards by means of air-borne conidia northward from well-defined sources of spores have been observed. For three disease gradients studied in 1939 the mean levels of blossom infection in trees 22, 44, 66, and 88 feet from the nearest source trees were 39, 21, 12, and 6.5 percent, respectively, of the level in source trees. For four gradients studied in 1940 the corresponding values were 55.5, 40, 28, and 23.

The mathematical treatment of these data minimized or eliminated the effects of such factors as the number of spores produced and liberated at the source, the length of the dissemination periods, and variations in the environmental conditions that initiate infection. For this reason, an explanation of the difference between the 1939 and 1940 gradients was sought elsewhere. According to a study of the circumstances preceding blossom infection, in 1939 and again in 1940 there was only one period at the susceptible (blossoming) stage of the host when the direction of the wind favored spore dissemination northward from the source. During the 1940 period mean wind velocities

were 1.88 times higher than during the 1939 period. The amount of blossom infection was assumed to be proportional to the number of spores reaching the blossoms, and the unilateral characteristics of the gradients were judged to be expressions of variations in the aerial density of spores during the effective dissemination periods. Factors capable of disturbing the relations between incidence of the disease and aerial density of spores are discussed.

Variations in aerial density of spores as distance from the source of spores increased were studied by releasing *Lycopodium* spores and catching them on glass slides placed 5, 10, and 15 feet downwind from the point of release. The density—that is, the number of spores passing through a unit area of intercepting planes—varied approximately in inverse proportion to the square of the distance from the source, a relation to be expected if the dispersion of the spores is described by a horizontal cone having its apex at the source of spores and its base oriented to the direction of the mean wind.

According to other tests the over-all distribution of these spores along the vertical and horizontal axes of intercepting planes followed roughly that of normal probability; that is, the density of these bodies was greatest in the center of the plane (at the level of release) and decreased progressively above and below and to the right and left of the center. The standard deviations of the distributions were employed, therefore, to express the degree of dispersion at various distances from the source. These values increased approximately in proportion to the distance from the source. At equivalent distances, however, the standard deviation for horizontal distributions (σ_h) were consistently greater than those for vertical distributions (σ_v). When spores were released 7.5 feet from the ground, the mean σ_h/σ_v ratio was found to be 1.55, a value very close to 1.59, the figure obtained by others in measuring the amplitude of the horizontal and vertical components of turbulence by means of the bidirectional wind vane placed 6.56 feet from the ground. Studies of the dispersion of small puffs of ammonium chloride "smoke" gave similar results.

The effect of trees (without leaves) on vertical dispersion of spores was studied.

The rate at which aerial density of spores decreased with increases in distance from the source was apparently not affected by variations in wind velocity between 2 and 16 miles per hour. For winds of low velocity (below about 5 miles per hour), however, dispersion at a given distance from the source was often greater than that for medium and high velocity. Between medium and high velocities, on the other hand, dispersion varied little within the distances studied (5 to 15 feet).

Since frictional turbulence increases with wind velocity, aerial dispersion of spores should likewise increase, other things being equal. The degree of dispersion at a given distance from the source, however, is determined by the rate the spores are dispersed in relation to the rate they are carried downwind. When the source is a limited area at least, the degree of spore dispersion at a given distance will probably decrease as wind velocity increases—unless the effects of turbulence on dispersion increase as fast as wind velocity, or faster. On the whole, the experimental results indicate that dispersion increased at about the same rate as velocity, except at velocities below about 5 miles per hour; but further study of this point is desirable. In par-

ticular, dissemination should be studied at distances from the source greater than those employed herein.

To compare the results from observations on disease spread with those from the experiments, the latter were generalized in terms of dissemination (1) from a three-dimensional block source instead of from a "point" source, (2) through orchard trees instead of over open ground, and (3) for distances up to 100 feet instead of 15 feet. Certain gaps were bridged by assumptions, which, if rendered untenable by further studies, can be modified to conform with the new information. Though the results of this treatment must remain provisional, the observed spread of the disease through the apricot orchards is described to a good first approximation by an equation of the form $y=\frac{A}{x^p}$, where y is the ratio of the percentage of blossom infection in a vertical slice of susceptible tissue (blossom) at a horizontal distance from the source block to the percentage of blossom infection in the source trees, A and p are constants depending on wind velocity and perhaps on other quantities to a lesser extent, and x is the horizontal distance from the center of the nearest source trees.

LITERATURE CITED

(1) Boevsky, A. S.
1936. The spread of Puccinia triticina in the wheat fields. *In* [Leningrad] Inst. Zashch. Rast. (Lenin Acad. Agr. Sci. U. S. S. R., Inst. Plant Protect.) Summary of the Scientific Research Work in the Institute of Plant Protection. Ser. 3, 1935: 111–116. [In Russian.]

(2) Brunt, D.
1934. Physical and dynamical meteorology. 411 pp., illus. London.

(3) Carver, H. C.
1924. Frequency curves. *In* Rietz, H. L., ed. Handbook of Mathematical Statistics. pp. 92–119. Cambridge, Mass.

(4) Geiger, R.
1927. Das klima der bodennahen luftschicht. Wissenschaft 78. Braunschweig. (Translated by John [B.] Leighly in O. P. 165–2–42–180. 1942. Works Projects Administration in Ohio.)

(5) Gregory, P. H.
1945. The dispersion of air-borne spores. Brit. Mycol. Soc. Trans. 28: 26–72. illus.

(6) Heald, F. D., Gardner, M. W., and Studhalter, R. A.
1915. Air and wind dissemination of ascospores of the chestnut-blight fungus. Jour. Agr. Res. 3: 493–526, illus.

(7) Jacobs, W. C.
1939. A discussion of physical factors governing the distribution of microorganisms in the atmosphere. Jour. Mar. Res. 2: 218–224.

(8) Kalinske, A. A.
1940. Relation of the statistical theory of turbulence to hydraulics. Amer. Soc. Civil Engin. Trans. 105: 1547–1600, illus.

(9) Lampert, E. B.
1929. The relation of weather to the development of stem rust in the Mississippi valley. Phytopathology 19: [1]–71, illus.

(10) Lyman, H.
1918. Smoke from the Minnesota forest fires. U. S. Dept. Agr. Monthly Weather Rev. 46: 506–509, zillus.

(11) McCubbin, W. A.
1918. Dispersal distance of urediniospores of cronartium ribicola as indicated by their rate of fall in still air. Phytopathology. 8: 35—36, illus.

(12) MOULTON, F. R., ed.
1942. AEROBIOLOGY. Amer. Assoc. Adv. Sci. Pub. 17, 289 pp., illus. Lancaster, Pa.
(13) NEWHALL, A. G.
1938. THE SPREAD OF ONION MILDEW BY WIND-BORNE CONIDIA OF PERONOSPORA DESTRUCTOR. Phytopathology 28: 257–269, illus.
(14) OSGOOD, W. F.
1930. ADVANCED CALCULUS. 530 pp. New York.
(15) PETTERSSEN, S.
1941. INTRODUCTION TO METEOROLOGY. 236 pp., illus. New York.
(16) RITTENBERG, S. C.
1939. INVESTIGATIONS ON THE MICROBIOLOGY OF MARINE AIR. Jour. Mar. Res. 2: 208–217.
(17) SCHMIDT, W.
1918. DIE VERBREITUNG VON SAMEN UND BLÜTENSTAUB DURCH DIE LUFTBEWEGUNG. Österr. Bot. Ztschr. 67: 313–328, illus.
(18) STEPANOV, K. M.
1935. DISSEMINATION OF INFECTIOUS DISEASES OF PLANTS BY AIR CURRENTS. Leningrad Inst. Zashch. Rast. (Lenin Acad. Agr. Sci., U. S. S. R., Inst. Plant Protect.) Plant Protect. Ser. 2 (Phytopathology) 8: 1–68, illus. [In Russian with English summary.]
(19) UKKELBERG, H. G.
1933. THE RATE OF FALL OF SPORES IN RELATION TO THE EPIDEMIOLOGY OF BLACK STEM RUST. Torrey Bot. Club. Bul. 60: 211–228, illus.
(20) WILSON, E. E.
1942. EXPERIMENTS WITH ARSENITE SPRAYS TO ERADICATE SCLEROTINIA LAXA IN STONE-FRUIT TREES AS A MEANS OF CONTROLLING THE BROWN ROT DISEASE OF BLOSSOMS. Jour. Agr. Res. 64: 561–594, illus.

U. S. GOVERNMENT PRINTING OFFICE: 1946